

3.—The taxonomic status of small fossil thylacines (Marsupialia, Thylacinidae) from Western Australia

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Fossil thylacines from the Eucla Division of Western Australia have conspicuously smaller teeth than those of modern *Thylacinus cynocephalus*. With size of teeth the criterion, their taxonomic status is assessed using statistical comparisons that include a test developed by McNeil (see the Appendix). The tests show that for the Eucla Division fossil thylacines, the requirement of the "75 per cent rule" for subspecies is not met at a 95 per cent level of confidence. The Eucla Division fossil thylacines are therefore referred to *Thylacinus cynocephalus*. The re-evaluation of the taxonomic status of fossil thylacines from southwestern Australia, using the same tests, confirms Ride's (1964) conclusion that there is no justification for recognizing these fossils as a new subspecies. However, the heterogeneity of the sample leaves the status of those fossils uncertain. Sexual dimorphism is marked in *Thylacinus* and a statistical method is used to separate some Eucla Division fossil thylacines into presumed males and presumed females.

In the Appendix, McNeil shows that Ride's (1964) method of applying confidence intervals to Mayr's (1969) test for subspecies is invalid. McNeil develops a valid statistical process for testing for subspecies, for both small and large samples.

Introduction

During 1966 my husband and I discovered the skeletal remains of eight thylacines (Tasmanian "tigers" or "wolves") in a cave in the Eucla Land Division of Western Australia (Lowry and Lowry, 1967). These, and other fossil vertebrate remains were recovered for the fossil collection of the Geological Survey of Western Australia.

Later examination suggested that the thylacines were very small compared with modern *Thylacinus cynocephalus* from Tasmania, and thus the question arose whether they represented a different species or subspecies. To determine the taxonomic status of specimens from the Eucla Division, I have statistically compared selected dental characters with those of a sample of modern *T. cynocephalus*, and also a sample of fossil thylacines from caves in southwestern Western Australia. Ride (1964) showed that the fossils from southwestern Australia tended to be smaller than *T. cynocephalus*, but he considered them to be conspecific.

During the course of my analysis it appeared that some of the statistical techniques used by Ride (1964) should be re-examined (see the

Appendix), and hence a re-appraisal of the taxonomic status of the southwestern Australian fossils is given here. The analysis led to a consideration of sexual dimorphism in *Thylacinus*, which is discussed at the end of the paper, and a method of determining the sexes in a homogeneous sample is given.

The taxonomic assessment of fossil *Thylacinus* samples

Previous taxonomic assessment of fossil *Thylacinus*

Only one living species, *Thylacinus cynocephalus* (Harris) from Tasmania, is known. It was common until the beginning of the century, but it is now very rare, possibly extinct. On mainland Australia the genus is represented only by fossils.

Size has been a major criterion in separating the described species. Thus Krefft (1871) described *T. breviceps* from Tasmania as a small species, with larger teeth than *T. cynocephalus*, and Owen (1845) considered *T. spelaeus*, an eastern Australian fossil of the Pleistocene, as simply a larger thylacine than *T. cynocephalus*. Another eastern Australian Pleistocene fossil, *T. rostralis*, was described by De Vis (1894) as also being larger than the living species. The Tertiary fossil *T. potens* Woodburne from Alcoota, central Australia, is even more massive than both *T. spelaeus* and *T. rostralis* (Woodburne, 1967).

Other fossils from mainland Australia are mainly smaller in size than *T. cynocephalus*. The small thylacines from southwestern Australia mentioned above, which Ride (1964) considered conspecific with *T. cynocephalus*, are considered to be of late Quaternary age (Merri- lecs, 1968). Apart from the small thylacines recovered by Lowry and Lowry (1967), two further small examples have been recorded from the Eucla Division of Western Australia by Cook (1963) and Partridge (1967), with Partridge's specimen being 3,300 years old. Small fossils have twice been recorded outside Western Australia. A single tooth, 4,000 years old, was found in an excavation in a rock shelter at Fromms Landing, South Australia (Macintosh and Mahoney, 1964), and a small thylacine is known from Lake Menindee, New South Wales (Woodburne, 1967).

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Size as a taxonomic criterion in Thylacinus

Previous workers have mostly used size as a criterion for distinguishing thylacine species, and the present study therefore is limited to a consideration of size. The size of an individual thylacine depends in part on its maturity, a problem avoided by measuring and analysing selected tooth dimensions, assumed to remain constant throughout an individual's life. This choice is important because the individuals in the Eucla Division sample show a great range in maturity. Furthermore, post-cranial remains are relatively scarce in the southwestern Australian sample, and no data on post-cranial remains of modern *T. cynocephalus* were available.

There appear to be certain short-comings in some of the previous analyses of size differences between thylacines from various localities. The species concept of the early taxonomists, even if not classically "typological", did not emphasize interbreeding populations and reproductive isolation, as does the "biological" or "evolutionary" concept prominent today (Mayr, 1969), and a concept of a range of variation within a given species was often neglected. For example, *T. breviceps* was based on a sample of two specimens, and both *T. rostralis* De Vis and *T. breviceps* Krefft were compared with a single specimen of *T. cynocephalus*. As neither De Vis (1894) nor Krefft (1871) identify the specimen, it is not known if the same one was used on both occasions. Not surprisingly the validity of some of the species erected during that period has been questioned. Thus Stephenson (1963) considered that *spelaeus* should lapse into synonymy because he considered the differences in size between *T. spelaeus* and *T. cynocephalus* were negligible. This was demonstrated by Ride (1964), who showed that there was no statistically significant difference between mean values of selected dental characters. The short-comings mentioned above can be reduced by taking large samples and analysing them statistically because "the erection of a taxonomic subspecies, species or genus by inferring the nature and limits of corresponding morphological groups from a series of given specimens is essentially a statistical problem" (Simpson, 1943).

Since natural populations of sexually reproducing animals can be expected to differ from one area to another, it is not enough to simply find statistically significant differences between populations to establish a new species or subspecies (Mayr, 1969). The problem of intra-specific variation is more acute when a time element is introduced. The early workers on *Thylacinus* do not seem to have considered the possibility of intra-specific evolutionary changes involving body size, yet during the Quaternary many mammals have shown fluctuations in size (Hooijer, 1949; Kurtén, 1964, 1965, 1968), including much post-Pleistocene dwarfing. Because a short time is involved, Hooijer and Kurtén believed that the differences between the large Pleistocene forms and some of the smaller modern forms are often no more than subspecific. Thus size as a criterion for distinguishing between species of Quaternary mammals

should be used with caution. The Quaternary fossil thylacines may in fact have represented populations of larger and smaller individuals of a single species, that existed on the mainland at different periods of time. Ride (1964) claimed that differences between the small sized southwestern Australian fossils and *T. cynocephalus* were not great enough to warrant even subspecific recognition, but since the Eucla Division fossils appear to be even smaller, the possibility that they represented a subspecies of *T. cynocephalus*, rather than a new species, is considered.

The recognition of subspecies in small samples

Although the species category has objective reality (Simpson, 1943) the subspecies, like the higher categories, has subjective boundaries (Simpson, 1943; Amadon, 1949; Mayr, 1969). The subspecies category has been defined by Mayr (1969) as "an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species". Where there are clear-cut differences between two such populations, the recognition of subspecies is quite simple, but where their intra-population range of variation overlap, a "75 per cent rule" is often used to determine if enough difference exists to warrant recognition by name (Amadon, 1949). This rule or convention is subject to various interpretations, but it is usually required that 75 per cent of specimens in a sample from the proposed new subspecies must differ from "all" (97 to 99 per cent) specimens from all other previously recognised subspecies (Amadon, 1949; Mayr, 1969). The requirement of the rule is approximately met when 90 per cent (or more) is separable from 90 per cent (or more) of samples of all previously recognised subspecies (Mayr, 1969). It is also easier to calculate percentage separation when overlap is symmetrical.

The statistic Coefficient of Difference (abbreviated to CD) proposed by Mayr (1943) and discussed by Mayr (1969) attempts to show whether the requirement of the 75 per cent rule has been met. It is based on the observation that the degree of overlap of two curves is related to the difference of their mean divided by the sum of their standard deviations. With the aid of a table, CD can be used to show whether two samples are sufficiently separate for the populations they represent to be arbitrarily accorded subspecies status. Mayr (1969) gives a table of values of CD and the corresponding percentage separation. See also Table I in the Appendix by McNeil.

The advantage of CD is its simplicity and ease of calculation, but the statistic assumes that the populations are normally distributed, and that values of sample statistics equal those of population parameters; hence calculated values of CD can at best only give an indication of magnitude of overlap between two curves. In borderline cases, or where these assumptions cannot be made, such as when samples are small, a more accurate test is required.

Different authors require different values of CD to demonstrate subspecific separation, depending on their interpretation of the 75 per cent rule. Thus Mayr (1969) requires a value of at least 1.28, representing a separation of at least 90 per cent from 90 per cent, but others are more stringent, requiring up to 97 per cent separable from 97 per cent (Amadon, 1949), which is indicated by a CD value of 1.9. In his study of *Thylacinus*, Ride (1964) considered an intermediate value for CD of 1.5, representing a separation of about 94 per cent from 94 per cent, as adequate for the recognition of subspecies, but that a more stringent test should apply when samples are small, as were the fossil samples available to him. He therefore modified the statistic Coefficient of Difference as given by Mayr and others (1953) by calculating its 95 per cent confidence interval, and requiring a value of at least 1.5 for the lower limit.

Since this paper is in part a continuation and re-evaluation of Ride's (1964) work on *Thylacinus*, it seemed appropriate to extend his statistical approach to the analysis of the Eucla Division thylacines, and to require a value greater than 1.5 for lower confidence limits, when testing percentage separation of the fossils from *T. cynocephalus*. However, McNeil (see the Appendix) shows that Ride's (1964) modification is invalid, and gives the mathematical development of an accurate statistic to which confidence intervals can be applied. I therefore use this statistic and confidence interval, but follow Ride (1964) by requiring a value greater than 1.5 for the lower confidence limit to indicate adequate separation of samples to warrant subspecies recognition of the populations they represented. The 95 per cent confidence interval applied to the statistic developed by McNeil does not give as wide an interval as the one used by Ride (1964); hence I re-evaluate the taxonomic status of the southwestern Australian fossil thylacines. Also, a few more fossil specimens have been discovered since the publication of Ride's (1964) paper.

The use of normal statistics with samples of Thylacinus.

Thylacinus cynocephalus from Tasmania shows strong sexual dimorphism, with males tending to have larger teeth than females (Ride, 1964). Thus the distribution of dental characters from samples of *T. cynocephalus* tend to be bimodal. I have therefore applied χ^2 tests to the data from the sample of modern Tasmanian thylacines (the only one large enough for the meaningful use of this test), to check whether frequency distributions depart statistically significantly from normality, thus rendering tests based on this assumption invalid. The χ^2 probabilities are not significant, except for the length of the upper 2nd molar (M^2) and the length of the lower 4th molar (M_4). Hence results for these characters are doubtful.

Description of the *Thylacinus* samples.

The control sample of modern Thylacinus cynocephalus from Tasmania

Dr. W. D. L. Ride (Director, Western Australian Museum) has kindly made available to me many data (largely unpublished) on modern *T. cynocephalus*. These specimens are now lodged at widely separate institutions (see Ride, 1964), which prevented me from re-measuring them. To test my ability to reproduce Ride's measurements I re-measured those fossils in the Western Australian Museum originally measured by him, and applied a t-test (Simpson and others, 1960) to these paired data. The probability that my measurements and Ride's were the same ranged from greater than 50 per cent to greater than 70 per cent. Tooth dimensions are recorded to 0.1 mm, and since 0.1 mm amounts to only one or two per cent of the dimensions of the tooth measurements, I therefore consider comparisons of Ride's data with mine to be valid. Ride (1964) selected the data he published to exclude measurements from juveniles because some of the characters he used include bone and thus are affected by growth, but since I analyse only dental characters, I have included measurements from juveniles. Hence the values for calculated statistics that Ride (1964) records in his Tables 1 and 2 for the four dental characters I also use (M^2 , M^3 , M_4 , and P_4), are not precisely the same as the values I record in this paper.

The Eucla Division fossil Thylacinus sample

All fossil thylacines from the Eucla Division were found on the surface of the floors of caves (see figure 1 for the location of the caves). Cave numbers (e.g. N63 below) are those of the cave registration system of the Australian Speleological Federation. Specimen catalogue numbers like 64.8.1 refer to the fossil collection of the Western Australian Museum, and those like F6358 refer to fossils from the collection of the Geological Survey of Western Australia at present housed in the Western Australian Museum.

(i) From Thylacine Hole (N63)

Thylacine Hole (31° 42' S; 127° 44' E) is about 100 km west of Eucla, and lies on the Hampton Tableland, a semi-arid region characterised by grassy flats and tree-covered ridges. The cave has been described by Lowry and Lowry (1967) who recovered partial or complete skeletons representing eight different thylacines. One of them, F6364, is a remarkably preserved carcass, from which hair and soft tissue has been dated (NSW 28c) at $4,650 \pm 153$ years BP (Lowry and Merrilees, 1969; Merrilees, 1970). Five specimens, F6353, F6354, F6355, F6357 and F6358, are nearly complete skeletons that include measureable teeth. One specimen, F6356, does not include teeth, and another, F6360, consists only of the pelvis and part of the vertebral column. Measurements from the carcass F6364 are not included in the statistical sample because they could not be made accurately without damaging the specimen.

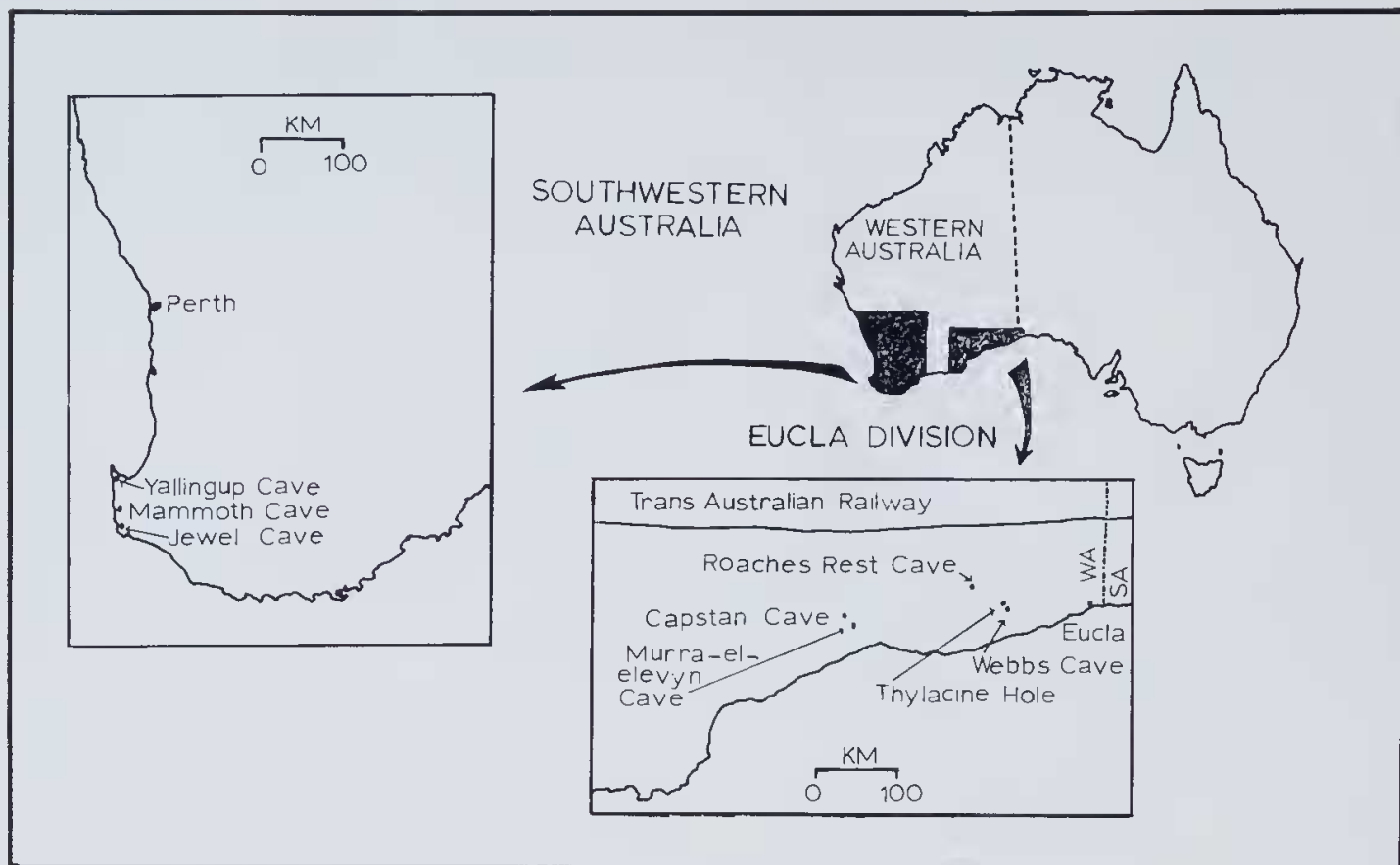


Figure 1.—Locality maps.

The remains represented animals in their death positions, except F6360 which had been disturbed by water wash. All had probably fallen nearly 12 metres through the sole narrow chimney-like entrance into the cave, yet only one specimen, F6355, has broken bones, and even this may have occurred after death through roof collapse of the cave. F6358 is a juvenile with the basioccipital—basipresphenoid and basipresphenoid—presphenoid sutures open, the upper fourth molars not erupted, and no perceptible wear on the teeth. In F6357 both these sutures are fused and the teeth are well worn. The other three specimens show intermediate stages of maturity.

(ii) From Murra-el-elevyn Cave (N47)

Murra-el-elevyn Cave ($32^{\circ} 03' S$; $126^{\circ} 02' E$) is about 6.4 km west of Cocklebidy Motel, on the Hampton Tableland. A single specimen, 64.8.1, with adhering soft tissue dated (GaK 693) $3,280 \pm 90$ years BP (Partridge, 1967) was recovered from the cave. All teeth are present.

(iii) From Roaches Rest Cave (N58)

Roaches Rest Cave ($31^{\circ} 33' S$; $127^{\circ} 14' E$) is about 45 km northwest of Madura, and lies on the tree-less Nullarbor Plain *sensu stricto*. The single specimen, 67.3.21, represented a juvenile, and consists of fragments of the lower jaw and skull. Some teeth are missing and others are not measurable.

(iv) From Capstan Cave (N50)

Capstan Cave ($32^{\circ} 01' S$; $125^{\circ} 57' E$) is about 14.5 km west of Cocklebidy Motel, on the Nullarbor Plain. The single specimen, 67.11.37, is a right dentary, and carries measurable first and third premolar and first molar teeth.

(v) From Webbs Cave (N132)

Webbs Cave ($31^{\circ} 46' S$; $127^{\circ} 50' E$) lies on the Hampton Tableland, and is near Thylacine Hole, about 90 km west of Eucla. Cook (1963) described a single upper molar, 70.7.54, from this cave. The specimen is mentioned again below, but is not included in my statistical sample because its position in the tooth row is not known with certainty.

The southwestern Australian fossil Thylacinus sample

The fossil sample from the southwest of Western Australia includes all specimens measured by Ride (1964, "Western Cave-fossil *Thylacinus*") and those discovered subsequently. Thus the values of calculated statistics I give in Tables 1, 2, and 3 for the dental characters M^2 , M^3 , M_1 and P_4 are not precisely the same as those recorded by Ride (1964). Most of the specimens came from caves formed in Quaternary eolianite in the extreme southwestern portion of Western Australia (Figure 1), such as Yallingup Cave (Ya 1), Mammoth Cave (Wi 38-39), and Jewel Cave (Au 13). Two specimens, 61.2.19-23 and 63.7.7, came from caves about 100 km north of Perth. Three of the specimens from the extreme southwest, 61.2.26, 61.2.27, and 61.2.28, came from Mammoth Cave, from a deposit which appears to be more than 37,000 years old (Lundelius, 1960; Merrilees, 1968). Merrilees (1968) considers these to be the oldest specimens available from Western Australia, but that even these are unlikely to be older than late Quaternary.

Statistical assessment of Western Australian fossil *Thylacinus*

Results and discussion of statistical tests

The statistical procedure I use to determine the taxonomic status of the fossil samples is similar to the one advocated by Ride (1964, Appendix). After applying χ^2 tests to check the normality of the data and F-tests to check that sample variances do not differ significantly, mean dimensions of dental characters are compared using a standard t-test. Those characters that give statistically significant values for t are tested for subspecies separation using the statistic developed by McNeil (see the Appendix). A value greater than 1.5 for the lower confidence limit is required to establish subspecies status.

The following dental characters were measured and tested. I follow Ride (1964) in nomenclature.

- (i) Upper molars 1 to 3 (M^1 to M^3)—diagonal length through protocone to metacone.
- (ii) Lower molars 1 to 4 (M_1 to M_4)—length.
- (iii) Lower premolars 1, 3, and 4 (P_1 , P_3 and P_4)—length.

Upper molars were measured along the longest diagonal crossing the protocone and metacone, and lower molars and premolars along the greatest length in an approximately antero-posterior direction. For consistency right teeth were chosen where possible, although they tend to be a little larger than teeth from the left side. This difference is not significant however. Of 153 pairs of measurements, the mean value of measurements from the right side is 10.21 mm and from the left side 10.18 mm. Copies of the raw data, together with an explanation of their

meaning and accuracy have been lodged in the libraries of the University of Tasmania, Hobart, and the Western Australian Museum, Perth.

Table 1 gives a summary of the dimensions of the dental characters tested, and shows that teeth from the Eucla Division fossils are generally smaller than those of the southwestern Australian fossils, and conspicuously smaller than those of modern *Thylacinus cynocephalus*. Standard tests of comparison were applied to all the data, despite the questionable normality of the lengths of M^2 and M_1 from the modern *T. cynocephalus* sample. Table 2 shows that results of standard tests applied to data from these two characters follow the same trends as those shown by the other characters, and hence can probably be accepted.

Results of F-tests are given in Table 2, and show that the sample variances generally do not differ between the three thylacine samples, excepting variances for the dimensions of P_4 and M_3 from the southwestern Australian fossils. Since in practice the t-test is a robust test (Simpson and others, 1960) it was also applied to these two characters.

Results of the t-tests are given in Table 2, and show that there is no statistically significant difference between mean dimensions of dental characters of the southwestern Australian and Eucla Division fossils at the one per cent level. All the tests between fossil samples and modern *T. cynocephalus* gave significant results at the one per cent level, except the mean dimension of the length of P_1 of the Eucla Division fossils. It is therefore worth testing whether the requirement of the 75 per cent rule for subspecies is met.

Table 1

Summary of dimensions of dental characters of the *Thylacinus* samples.

Character†	Modern <i>Thylacinus cynocephalus</i>					Southwestern Australian Fossil <i>Thylacinus</i>					Eucla Division Fossil <i>Thylacinus</i>				
	Mean X mm.	Observed Range mm.	n	s mm.	V	Mean X mm.	Observed Range mm.	n	s mm.	V‡	Mean X mm.	Observed Range mm.	n	s mm.	V‡
M^1	11.6	10.1-12.7 (2.6)	60	0.61	5.3	10.3	9.5-12.1 (2.6)	12	0.72	7.2	10.2	9.5-11.0 (1.5)	7	0.52	5.3
M^2	15.1	13.6-16.6 (3.0)	61	0.88	5.8	13.0	11.4-15.9 (4.5)	12	1.06	8.4	12.5	11.2-13.2 (2.0)	6	0.72	6.1
M^3	17.8	15.4-20.2 (4.8)	54	1.23	6.9	15.4	13.1-17.7 (4.6)	9	1.25	8.4	14.6	13.7-15.3 (1.6)	6	0.77	5.5
P_1	6.2	5.3-7.0 (1.7)	63	0.42	6.9	5.6	4.9-6.4 (1.5)	9	0.49	9.0	5.9	5.5-6.3 (0.8)	6	0.31	5.6
P_3	9.2	8.1-10.1 (2.0)	64	0.46	5.0	8.1	7.1-9.1 (2.0)	11	0.66	8.4	7.8	7.0-8.3 (1.3)	7	0.50	6.6
P_4	10.8	9.2-11.9 (2.7)	64	0.59	5.4	10.0	8.7-12.1 (3.4)	13	1.05	10.7	9.7	8.9-11.0 (2.1)	6	0.82	8.8
M_1	9.6	8.6-10.6 (2.0)	39	0.57	6.0	8.6	7.5-9.8 (2.3)	13	0.66	7.8	8.3	7.9-9.0 (1.1)	7	0.45	5.6
M_2	11.9	11.0-13.2 (2.2)	41	0.53	4.5	11.2	10.2-12.6 (2.4)	11	0.75	6.8	10.4	9.9-11.2 (1.3)	8	0.48	4.7
M_3	14.1	12.8-15.3 (2.5)	41	0.57	4.1	13.0	11.1-15.0 (3.9)	12	1.18	9.3	12.3	11.5-13.0 (1.5)	7	0.67	5.7
M_4	15.8	13.9-17.2 (3.3)	53	0.92	5.8	14.5	12.8-16.9 (4.1)	12	1.32	9.3	13.5	11.8-14.2 (2.4)	6	0.95	7.3

† Characters are described in the text on page 23.

‡ Coefficient of Variation corrected for small sample size using a correction developed by Haldane (1955).

Table 2

Results of standard tests of comparison.

Character†	Modern <i>Thylacinus cynocephalus</i> compared with Eucla Division fossil <i>Thylacinus</i>				Modern <i>Thylacinus cynocephalus</i> compared with southwestern Australian <i>Thylacinus</i>				Southwestern Australian fossil <i>Thylacinus</i> compared with Eucla Division fossil <i>Thylacinus</i>			
	F	p	t	Mean	F	p	t	Mean	F	p	t	Mean
M ¹	1.38	>0.2	5.55	<0.001**	1.40	>0.2	6.16	<0.001**	1.93	>0.2	0.35	0.8>x>0.7
M ²	1.47	>0.2	7.07	<0.001**	1.46	>0.2	7.34	<0.001**	2.14	>0.2	1.07	0.3>x>0.2
M ³	2.55	>0.2	6.20	<0.001**	1.04	>0.2	5.57	<0.001**	2.66	>0.2	1.25	0.3>x>0.2
P ¹	1.83	>0.2	1.57	0.2>x>0.1	1.34	>0.2	3.43	<0.001**	2.45	>0.2	1.09	0.3>x>0.2
P ²	1.18	>0.2	7.32	<0.001**	2.02	0.1>x>0.05	6.96	<0.001**	1.75	>0.2	0.79	0.5>x>0.4
P ³	1.94	0.2>x>0.1	4.04	<0.001**	3.26	<0.01**	3.66	<0.001**	1.64	>0.2	0.60	0.6>x>0.5
M ₁	1.61	>0.2	5.65	<0.001**	1.34	>0.2	5.20	<0.001**	2.15	>0.2	1.07	0.3
M ₂	1.24	>0.2	7.64	<0.001**	1.99	0.2>x>0.1	3.49	<0.001**	2.47	>0.2	2.84	0.02>x>0.01*
M ₃	1.36	>0.2	7.78	<0.001**	4.26	<0.01**	4.55	<0.001**	3.13	0.2>x>0.1	1.52	0.2>x>0.1
M ₁	1.07	>0.2	5.84	<0.001**	2.03	0.2>x>0.1	4.11	<0.001**	1.93	>0.2	1.65	0.2>x>0.1

† Characters are described in the test on page 23.

* Significant at the 5 per cent level.

** Significant at the 1 per cent level.

Results of the test developed by McNeil (see the Appendix) are given in Table 3, and show that no characters from the south-western Australian fossils achieve a significant value of greater than 1.5. Thus the use of a more accurate statistic, a larger sample, and the consideration of extra characters, does not alter Ride's (1964) conclusion that the southwestern Australian fossils are insufficiently separate from *T. cynocephalus* to warrant the creation of a new subspecies, let alone a new species.

The requirement of the 75 per cent rule is met in two dental characters (M² and M₃) from the Eucla Division fossil thylacines, but none of the lower 95 per cent confidence limits achieve this level of significance. Hence one cannot be sure that 94 per cent of the dimensions of these two characters will be separable from 94 per cent of those from modern *T. cynocephalus* in 95 per cent of all possible samples that might be taken from both populations. Since the data from modern *T. cynocephalus* on the length of M² is of questionable normality, the result of the test for this character would have been interpreted with caution, even if the lower confidence limit had achieved a statistically significant value. Accordingly, although the teeth of the Eucla Division fossils are significantly smaller, this is an inadequate reason for separating them from *Thylacinus cynocephalus*.

Although the criterion of mean size indicates that the southwestern Australian fossil thylacines should be referred to *T. cynocephalus*, their status is not clear because of the heterogeneity of the sample. This is demonstrated by a high Coefficient of Variation (V) and also a large observed range of variation (Table 1). The mean dimensions given in Table 1 mask the fact that there are four individual specimens from the southwestern Australian sample with tooth dimensions exceeding the mean values of the modern *T. cynocephalus* sample, and that there are five individual specimens with tooth dimensions below the mean values of the Eucla Division sample. Two of the large specimens came from Mammoth Cave, and thus are probably late Pleistocene in age (see above). Until more specimens that can be dated are found from both the southwest of Western Australia and the Eucla Division, there is no way of deciding between three alternatives:—(1) there were two species, a smaller and a larger in southwestern Australia; (2) the size range illustrates an intra-specific post-Pleistocene trend to size reduction in *Thylacinus* in southwestern Australia, as seen in some other mammals (see above); (3) the southwestern Australian fossil thylacines were simply more variable than other populations.

The taxonomic status of the thylacine tooth from Webbs Cave (N132)

The Webbs Cave tooth, 70.754, was not included in the Eucla Division statistical sample because the position in the tooth row of an isolated tooth is difficult to determine with certainty, but Cook (1963) is probably correct in calling it a left upper 3rd molar. The tooth has a length of 12.8 mm, which is considerably smaller than the mean dimension of 14.6 mm for upper 3rd molars from the Eucla Division sample, but a t-test gives a probability of just

over 5 per cent that it could have come from the Eucla Division population. I therefore refer this molar, assuming it to be an upper 3rd molar, to the Eucla Division fossil thylacines, and hence to *T. cynocephalus*.

Sexual dimorphism in *Thylacinus*

Modern *T. cynocephalus*, as mentioned above, shows strong sexual dimorphism. Ride (1964) showed that tooth dimensions of modern thylacines of known sex tend to fall into two groups, with those of males being larger than those of females. Thus where the sex of an individual specimen is unknown, its possible sex could be determined by comparing its tooth dimensions with those from other specimens from the same population.

Table 3

Test for subspecies

Character†	Southwestern Australian Fossil <i>Thylacinus</i>		Eucla Division Fossil <i>Thylacinus</i>	
	CD	CD ₁ *	CD	CD ₁ *
M ¹	0.97	0.68	1.11	0.74
M ²	1.16	0.85	1.51*	1.10
M ³	1.00	0.67	1.33	0.93
P ₁	0.61	0.31	0.33	0.02
P ₃	1.14	0.83	1.46	1.07
P ₄	0.53	0.30	0.86	0.49
M ₁	0.83	0.54	1.16	0.78
M ₂	0.59	0.30	1.48	1.07
M ₃	0.75	0.45	1.59*	1.16
M ₄	0.66	0.38	1.26	0.85

† Characters are described in the text on page 23.

* Significant result.

Table 4

*Determination of sex in fossil *Thylacinus* from Thylacine Hole*

Specimen Numbers	Ranks*					Score†
	1 (smallest)	2	3	4	5 (largest)	
F6358 ...	5	3	1	14
F6354 .	4	4	1	15
F6353	3	5	1	34
F6355	3	4	2	35
F6357 ...	1	1	1	3	3	33

* Rank columns record the frequency with which characters from each specimen were accorded a particular rank.

† Score column records the sum of the products of the ranks and frequencies for each specimen, and is a numerical expression of the visual assessment of its size, relative to the other specimens.

As with modern *T. cynocephalus*, the tooth dimensions of five specimens from Thylacine Hole also tend to fall into two groups, which could represent sexes. The following method considered all ten measured characters simultaneously in establishing the grouping of the fossils. Dimensions of dental characters were ranked from 1 (smallest) to 5 (largest) and the "rank" columns in Table 4 record the frequency with which the dimensions of characters from each specimen were accorded a particular rank. The "score" column in Table 4 records the sum of the products of the ranks and frequencies, for each specimen. For example, F6358 ranked smallest for the dimensions of 5 characters, second smallest for the dimensions of 3 characters and third in size for one character, and has a score of $5 \times 1 + 3 \times 2 + 1 \times 3 = 14$. This is a numerical expression of the visual observation that its teeth are the smallest of the five Thylacine Hole fossils. Table 4 records two specimens with small teeth (scores under 20) and three with large teeth (scores over 30). I suggest this grouping represents females and male respectively, from a population that on the whole had smaller teeth than the modern Tasmanian thylacine population.

It is possible to argue that the fossils from Thylacine Hole represented two species, one with smaller teeth than the other, but this seems unlikely because modern *Thylacinus* is known to show strong sexual dimorphism (Ride, 1964), and also, the pattern obtained by ranking the dimensions of their teeth indicates that the ratios of tooth measurements within an individual specimen are similar for each of the specimens. A concept of two sexes in a single species is more consistent with this observation than one of two species that lived in the area.

The best preserved fossil thylacine specimen from Thylacine Hole, F6364, was not included in Table 4 because only a few of its teeth could be measured without damaging the desiccated vibrissae, tongue and lips, but I have "ranked and scored" those measurements available from F6364 with corresponding measurements from the other tooth-bearing Thylacine Hole specimens. Its score groups with the two presumed females, and so the carcass probably represented a female.

The determination of the possible sex of an isolated specimen is more complex because thylacine samples from various places on the Australian mainland all have teeth of different mean dimensions. Thus the suggestion by Partridge (1967), that the specimen from Murra-el-elevyn Cave, 64.8.1 might have represented a female on the basis of its small teeth when compared with mean values for dental characters from the southwestern Australian fossils, cannot now be supported. Subsequent discoveries have shown that the teeth of all thylacines known from the Eucla Division tend to be smaller than mean values for teeth from the southwestern Australian fossils. Furthermore, the method described above apparently can only be used with specimens from the same local population. When tooth dimensions of 64.8.1 are "ranked and scored" with the five

Thylacine Hole specimens, its score is found to lie exactly between those of the presumed males and females, and thus its sex remains uncertain.

Similarly, the sex of the thylacine represented by 70.7.54, the Webbs Cave tooth (Cook, 1963), cannot be determined with certainty because dimensions of several characters from the one specimen need to be assessed simultaneously during the comparisons. However, assuming that the tooth is an M³, it is the smallest I have measured, and hence may have represented a female, as suggested by Cook (1963).

Acknowledgements

I wish to thank Dr. W. D. L. Ride (Director, Western Australian Museum) for freely making available much original information on modern *T. cynocephalus*; for explaining his measuring procedures; for access to Museum material; and for the use of Museum facilities. Thanks are also due to Dr. D. L. McNeil (Statistics Department, Princeton University) for kindly providing the Appendix, and giving me valuable advice on statistical procedures. Dr. N. A. Goodchild (Institute of Agriculture, University of Western Australia) has also given me statistical advice. I would also like to thank Dr. D. Merrilees (Western Australian Museum), and my husband Mr. D. C. Lowry (Geological Survey of Western Australia) for their kind help and valuable criticism.

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Appendix: Statistical Methodology for Subspecific Separation of Two Populations

By D. R. McNeil

The Coefficient of Difference

Suppose we have two populations of individuals, and X is a characteristic (such as the height of an individual). Let X_1 and X_2 represent the characteristics for individuals from the first and second population, respectively. Suppose also that X_1 and X_2 are normally distributed random variables, with expectations μ_1 , μ_2 and variances σ_1^2 , σ_2^2 , respectively. Put

$$(1) \quad F_i(x) = \text{Probability that } X_i \leq x, i = 1, 2.$$

Then $F_i(x)$ is the probability that the characteristic of an individual chosen at random from population i will not exceed x . $F_i(x)$ is called the cumulative probability distribution of X_i , and may be written

$$(2) \quad F_i(x) = \int_{-\infty}^x f_i(z) dz, i = 1, 2,$$

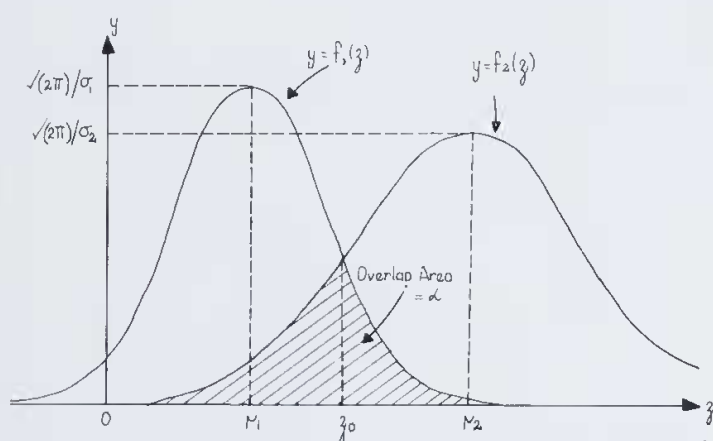
where $f_i(z)$ is the normal probability density function, i.e.

$$(3) \quad f_i(z) = (2\pi\sigma_i^2)^{-1/2} \exp\left\{-\frac{1}{2}\left(\frac{z - \mu_i}{\sigma_i}\right)^2\right\}, i = 1, 2.$$

The graphs of $f_1(z)$ and $f_2(z)$ are depicted in Figure 1.

If one is interested in measuring the difference between the two populations on the basis

of the characteristic X , a suitable measure must be defined. For definiteness let us assume that $\mu_2 > \mu_1$.



Appendix Figure 1.—Curves of the probability densities of the characteristic X , for the two populations, the variances (σ_1^2 and σ_2^2) being unequal.

One such measure is $\mu_2 - \mu_1$, the difference in the expectations of X for the two populations. Another is the *proportion of overlap* between the two populations, defined as the shaded area in Appendix Figure 1. If z_0 is the point at which the two curves intersect, then the proportion of overlap is obtainable by integration as

$$a = \int_{-\infty}^{z_0} f_2(z) dz + \int_{z_0}^{\infty} f_1(z) dz,$$

$$(4) \quad = F_2(z_0) + 1 - F_1(z_0).$$

A third measure of the difference between the two populations is the *coefficient of difference*

$$(5) \quad CD = \frac{\mu_2 - \mu_1}{\sigma_1 + \sigma_2},$$

which is commonly used in zoology (see, for example, Mayr, 1969, p. 189).

If the two populations have the same variance, then $\sigma_1 = \sigma_2 = \sigma$, say, and, using (3), z_0 is given by the (necessarily unique) point where the curves intersect.

Putting $f_1(z_0) = f_2(z_0)$ we get

$$(2\pi\sigma^2)^{-1/2} \exp\left\{-\frac{1}{2}\left(\frac{z_0 - \mu_1}{\sigma}\right)^2\right\}$$

$$= (2\pi\sigma^2)^{-1/2} \exp\left\{-\frac{1}{2}\left(\frac{z_0 - \mu_2}{\sigma}\right)^2\right\}.$$

Solving for z_0 we get $(z_0 - \mu_1)^2 = (z_0 - \mu_2)^2$, so that $z_0 = \frac{1}{2}(\mu_1 + \mu_2)$. Putting this in (4), we find

$$(6) \quad a = \int_{-\infty}^{\frac{1}{2}(\mu_1 + \mu_2)} (2\pi\sigma^2)^{-1/2} e^{-\frac{1}{2}(z - \mu_2)^2/\sigma^2} dz$$

$$+ 1 - \int_{-\infty}^{\frac{1}{2}(\mu_1 + \mu_2)} (2\pi\sigma^2)^{-1/2} e^{-\frac{1}{2}(z - \mu_1)^2/\sigma^2} dz.$$

The right-hand side of equation (6) may be reduced after some simplification to

$$(7) \quad a = 2\Phi\left(-\frac{\mu_2 - \mu_1}{2\sigma}\right),$$

where $\Phi(x)$ is the standardized normal cumulative distribution function, i.e.,

$$\Phi(x) = \int_{-\infty}^x (2\pi)^{-1/2} \exp(-\frac{1}{2}z^2) dz.$$

But in the case $\sigma_1 = \sigma_2 = \sigma$, the coefficient of difference is, using (5),

$$(8) \quad CD = \frac{\mu_2 - \mu_1}{2\sigma},$$

so that when the variances of the two populations are equal, the proportion of overlap and the coefficient of difference are related by the formula

$$(9) \quad a = 2\Phi(-CD).$$

It may be noted that as CD increases from 0 to ∞ , a decreases from 1 to 0. (This can be seen by inspection of Figure 1.) Thus, the larger the value of the coefficient of difference, the smaller the proportion of overlap between the two populations. Some values of a corresponding to various values of CD are given in Appendix Table 1. Thus a value of $CD = 1$ corresponds to a 32% overlap, that is, 16% of the first population are indistinguishable from 16% of the second. A value of $CD = 2$ corresponds to only 2.3% of the first population being indistinguishable from 2.3% of the second. A discussion of the relationship between a and CD is also given by Mayr (1969, p. 190).

Description of Ride's Method

In order to determine whether or not two populations are sufficiently different to warrant separate classification, zoologists have suggested that the CD be used as a measure, but have disagreed on the value required. In practice, it is not possible to measure CD exactly, since one usually has only a small sample of observations of X_1 and X_2 , and consequently any estimates of CD will be subject to sampling error. In a situation like this it is customary to obtain a confidence interval for CD . Such an interval can then be said to contain CD with a specified degree of certainty (usually 95%). If the interval obtained is wholly above the minimum value

Appendix Table 1

Values of the proportion of overlay, α , corresponding to the coefficient of difference, CD .

CD	0.50	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00
α	0.62	0.32	0.21	0.13	0.08	0.046	0.024	0.012	0.006	0.002

of CD which is sufficient for separate classification of the populations, then one can say that the populations are separate.

The problem of obtaining a confidence interval for the coefficient of difference has already been considered by Ride (1964), who gives as a 95% confidence interval (CD_1 , CD_2), where

$$CD_1 = \frac{[\bar{x}_2 - t_2 s_2 n_2^{-1/2}] - [\bar{x}_1 + t_1 s_1 n_1^{-1/2}]}{[(n_1 - 1)^{1/2} s_1 / \chi_{11}] + [(n_2 - 1)^{1/2} s_2 / \chi_{21}]}$$

$$CD_2 = \frac{[\bar{x}_2 + t_2 s_2 n_2^{-1/2}] - [\bar{x}_1 - t_1 s_1 n_1^{-1/2}]}{[(n_1 - 1)^{1/2} s_1 / \chi_{12}] + [(n_2 - 1)^{1/2} s_2 / \chi_{22}]}$$

and:

\bar{x}_1 and \bar{x}_2 are the two sample means
 s_1^2 and s_2^2 are the two sample variances
 n_1 and n_2 are the sample sizes
 t_1 and t_2 are the 0.975 quantiles of the Student t-distribution with $n_1 - 1$ and $n_2 - 1$ degrees of freedom, respectively

χ_{11}^2 (χ_{12}^2) and χ_{21}^2 (χ_{22}^2) are the 0.025 (0.975) quantities of the chi-squared distribution with $n_1 - 1$ and $n_2 - 1$ degrees of freedom, respectively.

Ride suggests that if both CD_1 and CD_2 are 1.5 or greater the two populations warrant subspecific separation, if neither reaches 1.5 it is probable that the populations are not subspecifically distinct, while if CD_1 is less than 1.5 and CD_2 1.5 or more further data is necessary to reach a conclusion.

The above procedure is invalid for two reasons:

- (i) Since the higher the value of the coefficient of difference, the more distinct are the two populations, a one sided confidence interval of the form (CD_1, ∞) is required. In statistical terms, one is testing the null hypothesis

$$H_0: CD < 1.5$$

against the one-sided alternative

$$H_1: CD \geq 1.5,$$

and the larger the value of the calculated coefficient of difference, the greater the evidence in favour of H_1 . In practice, it is not possible to test H_0 against H_1 , since H_0 is not a simple hypothesis (including as it does a whole range of values of CD). Therefore one replaces this range of values by the largest allowable value of CD which is not sufficient to warrant subspecific separation, namely 1.5. We then test

$$H_0: CD = 1.5$$

against

$$H_1: CD > 1.5,$$

and high values of the sample coefficient of difference, i.e. those in an interval of the form (CD_1, ∞), are significant.

- (ii) In obtaining the upper and lower points CD_2 and CD_1 , Ride has stated that the lower point of the confidence interval for the ratio $(\mu_2 - \mu_1) / (\sigma_1 + \sigma_2)$ is obtained by combining the lower point for the numerator with the upper point for the denominator (and similarly for the upper point of the confidence interval). This procedure would be valid if $\bar{x}_2 - \bar{x}_1$ and $s_1 + s_2$ were perfectly

negatively correlated with each other. To obtain a confidence interval for $(\mu_2 - \mu_1) / (\sigma_1 + \sigma_2)$ one must obtain the distribution of the ratio $(\bar{x}_2 - \bar{x}_1) / (s_1 + s_2)$, considering the joint distribution of $\bar{x}_2 - \bar{x}_1$ and $s_1 + s_2$. As a result, Ride obtains confidence intervals which are much wider than they should be.

We now give a valid statistical procedure for testing for subspecies.

Estimation of Coefficient of Difference and Statistical Inference

If $\sigma_1 \neq \sigma_2$, it is difficult to relate the CD value to the proportion of overlap. Moreover, unless $\sigma_1 = \sigma_2$, it is not possible to obtain exact statistical procedures for making inferences concerning the value of CD. Since in practice it is difficult to reject the hypothesis that $\sigma_1 = \sigma_2$ (using an F-test based on s_1/s_2 , values vastly different from unity being significant) we will proceed on the basis that the population variances are equal.

Assuming that $\sigma_1 = \sigma_2$, and given samples $(x_{1i}, i = 1, 2, \dots, n_1)$, $(x_{2i}, i = 1, 2, \dots, n_2)$ of n_1 values of X_1 and n_2 values of X_2 , the usual estimator of CD is

$$(10) \quad \hat{CD} = \frac{\bar{x}_2 - \bar{x}_1}{2s},$$

where \bar{x}_1 and \bar{x}_2 are the sample means and s is the (pooled) sample standard deviation, i.e.

$$s^2 = \{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2\} / (n_1 + n_2 - 2),$$

$$(11) =$$

$$\frac{1}{n_1 + n_2 - 2} \left\{ \sum_{i=1}^{n_1} (x_{1i} - \bar{x}_1)^2 + \sum_{i=1}^{n_2} (x_{2i} - \bar{x}_2)^2 \right\}.$$

Now it follows from (10) after some manipulations, that

$$\hat{CD} - \phi_1 - \alpha \left\{ \frac{n_1 + n_2}{4n_1 n_2} + \frac{(\hat{CD})^2}{2(n_1 + n_2 - 2)} \right\}^{1/2}.$$

$$\frac{\bar{x}_2 - \bar{x}_1 - (\mu_2 - \mu_1)}{(\sigma^2/n_1 + \sigma^2/n_2)^{1/2}} + \left(\frac{4n_1 n_2}{n_1 + n_2} \right)^{1/2} \frac{\mu_2 - \mu_1}{2\sigma} \\ \frac{\{ (n_1 + n_2 - 2)s^2/\sigma^2 \}^{1/2}}{(12) =}$$

$$\frac{1}{\beta} (n_1 + n_2 - 2)^{1/2} \cdot \frac{X + \beta(CD)}{\chi_{n_1 + n_2 - 2}} = \frac{1}{\beta} t\{\beta(CD)\},$$

where X has a standardized normal distribution, $\chi^2_{n_1 + n_2 - 2}$ has an independent chi-squared distribution with $n_1 + n_2 - 2$ degrees of freedom, and $\beta = \sqrt{4n_1 n_2 / (n_1 + n_2)}$. Thus $\beta \hat{CD}$ has a non-central t-distribution (see, for example, Keeping, 1962, p. 190) with $n_1 + n_2 - 2$ degrees of freedom and noncentrality parameter $\beta(CD)$. Using standard tables of the non-central t-distribution (see, for example, Resnikoff and Lieberman, 1957) one can now obtain a confi-

dence interval for CD. The procedure is as follows.

- (i) Calculate $\hat{\beta}CD$ from the sample.
- (ii) Determine, from the tables, the value of the non-centrality parameter $\beta(CD_1)$, say such that $\Pr\{t\{\beta(CD_1)\} < \hat{\beta}CD\} = 1 - \alpha$.
- (iii) The $(1 - \alpha)\%$ confidence interval for CD is then (CD_1, ∞) . (If $\alpha = 0.05$, a 95% confidence interval will be obtained.)

The procedure is now to accept subspecific classification if CD_1 is greater than 1.5 (say), with $(1 - \alpha)\%$ certainty of being correct.

Large Sample Theory

If n_1 and n_2 are moderately large one can obtain an approximate confidence interval for CD without use of tables. This is based on the

fact that \hat{CD} , suitably scaled, has a limiting standardized normal distribution as n_1 and n_2 tend to infinity. Using the law of large numbers, $\bar{x}_2 - \bar{x}_1 \rightarrow \mu_2 - \mu_1$ and $s \rightarrow \sigma$ as n_1 and $n_2 \rightarrow \infty$, so that

$$E[\hat{CD}] \rightarrow \frac{\mu_2 - \mu_1}{2\sigma} = CD$$

as $n_1, n_2 \rightarrow \infty$. Similarly it is possible to show that

$$\text{var}[\hat{CD}] \sim \frac{n_1 + n_2}{4n_1 n_2} + \frac{(CD)^2}{2(n_1 + n_2 - 2)},$$

as $n_1, n_2 \rightarrow \infty$. Since $\{\hat{CD} - CD\} / \{\text{var}[\hat{CD}]\}^{1/2}$ is asymptotically standardized normally distributed, an approximate $(1 - \alpha)\%$ confidence interval for CD is (CD_1^*, ∞) , where

$$(13) \quad CD_1^* =$$

$$\hat{CD} - \left\{ \frac{(n_1 + n_2 - 2)(n_1 + n_2)}{4n_1 n_2} \right\}^{1/2}$$

and $\phi_{1-\alpha}$ is the $1 - \alpha$ quantile of the standardized normal distribution. In particular a 95% confidence interval is given by $\phi_{0.95} = 1.64$.

An indication of the exactness of the asymptotic approximation (13) is given by comparing CD_1^* and CD_1 for moderate values of n_1 and n_2 . These values were checked and found to be in close agreement for the data analysed in Table 1 in the preceding article. For example, for the characteristic M_1 , in the case of the two populations "Modern *Thylacinus cynocephalus*" and "Eucla Division Fossil *Thylacinus*", it was found that at the 95% level $n_1 = 39$, $n_2 = 7$, $\hat{CD} = 1.16$, $CD_1 = 0.76$, $CD_1^* = 0.78$.

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Obituary

Eric Mervyn Watson 1903-1971

An Honorary Member and former President of the Royal Society of Western Australia, Dr. Eric Mervyn Watson, died at Augusta on September 7th, 1971 at the comparatively early age of 68. In addition to his period of office as President (1943-1944), Dr. Watson was Treasurer of the Society for ten years, and a member of the Council from 1936 to 1952.

Entering the University of Western Australia in 1922 from Perth Modern School, Eric Watson majored in Chemistry, completing his first degree in 1924 and an Honours degree in 1925. He was a student under Professor N. T. M. Wilsmore, and one of many graduates of that era who reached the top levels of the profession. After several positions as an industrial chemist, and temporary lecture-ships at the University of Adelaide and the University of Western Australia, he joined the teaching staff of Perth Technical College in 1929, and spent the remainder of his working life in that institution. Initially appointed an Assistant Lecturer, he rose through the various grades of Lecturer to be head of the Chemistry Department in 1946. During this time he became recognized as an authority on the training of chemists and pharmacists, and was honoured by election to Fellowships of both the Royal Australian Chemical Institute, and the Pharmaceutical Society of Victoria.

In 1930, soon after his appointment at Perth Technical College, Eric Watson was awarded a Hackett Studentship, which enabled him to study at Imperial College in the University of London for a degree of Doctor of Philosophy in the field of organic chemistry. Returning to the College in 1933, he began using the limited research facilities at his disposal to make studies in the chemistry of some Western Australian plants, in particular the eucalypts, and published the results in the *Journal of the Royal Society of Western Australia*. Although World War II ended this work the knowledge gained was valuable when he became a member of the Western Australian Drug Panel, which was set up to seek alternative sources for a number of pharmaceutical preparations which had been cut off because of hostilities. He was also active in Air Raid Precaution work, lecturing in chemical defence.

From the time he returned from London in 1933, Dr. Watson became increasingly involved in the teaching of Pharmacy students. Pharma-

cology had become a more exact science, and many of the older drugs in the form of plant extracts were being dropped in favour of pure organic chemicals. Pharmacists required a better knowledge of organic chemistry and biochemistry, and Dr. Watson was called on to supply it. He became keenly interested in raising the standard of education in pharmacy, but was also closely involved in establishing various Associateship courses in chemistry at Perth Technical College as qualifications for technologists in industry. In the later years of his career he was responsible for the initial planning of the Chemistry Department at the new Institute of Technology at Bentley.

To the staff of the College who knew him well, Eric Watson was recognized as an outstanding personality. His scholarship, his skill in organising, his ability as a lecturer, and his general capacity for getting things done, earned the respect of all his colleagues. He had little time for educational theorists, and none at all for "red tape" and other administrative tangles.

His students found him a teacher whose material was always well prepared, and whose chemical knowledge was encyclopaedic. He had the reputation of setting a very high standard, but whether or not this was so, at least his students could hold their own in the outside world, and many of them rose to high positions in their professions.

A few years after becoming head of the Chemistry Department Dr. Watson suffered a severe heart attack, and although he made a good recovery, care had to be observed in the years that followed. This involved curtailment of many of his activities, including membership of the Royal Society Council. He sought no further promotion in the College, and retired in 1963 in his 60th year. An active sportsman in his early years, he retained a strong interest in fishing, and spent the last eight years of his life in retirement at Augusta where he could indulge in his hobby. Even then he could not completely drop his active intellectual pursuits, and with his wife was instrumental in setting up a branch of the Western Australian Historical Society at Augusta, of which he was the first President.

The sympathy of all members of the Royal Society go to his widow, Mrs. Rose Watson, and to his son and daughter.